Composition of Fish Communities in a European Macrotidal Salt Marsh (the Mont Saint-Michel Bay, France)

P. Laffaille[a], E. Feunteun and J.-C. Lefeuvre

Laboratoire d'Evolution des Systèmes Naturels et Modifiés, UMR 6553 ' EcoBio ', Université de Rennes 1, Campus Beaulieu, 35042 Rennes cedex, France

At least 100 fish species are known to be present in the intertidal areas (estuaries, mudflats and salt marshes) of Mont Saint-Michel Bay. These and other comparable shallow marine coastal waters, such as estuaries and lagoons, play a nursery role for many fish species. However, in Europe little attention has been paid to the value of tidal salt marshes for fishes. Between March 1996 and April 1999, 120 tides were sampled in a tidal creek. A total of 31 species were caught. This community was largely dominated by mullets (*Liza ramada* represent 87% of the total biomass) and sand gobies (*Pomatoschistus minutus* and *P. lozanoi* represent 82% of the total numbers). These species and also *Gasterosteus aculeatus*, *Syngnathus rostellatus*, *Dicentrarchus labrax*, *Mugil* spp., *Liza aurata* and *Sprattus sprattus* were the most frequent species (>50% of monthly frequency of occurrence). In Europe, salt marshes and their creeks are flooded only during high spring tides. So, fishes only invade this environment during short immersion periods, and no species can be considered as marsh resident. But, the salt marsh was colonized by fish every time the tide reached the creek, and during the short time of flood, dominant fishes fed actively and exploited the high productivity. Nevertheless, this study shows that there is little interannual variation in the fish community and there are three ' seasons ' in the fish fauna of the marsh. Marine straggler and marine estuarine dependent species colonize marshes between spring (recruitment period in the bay) and autumn before returning into deeper adjacent waters. Estuarine fishes are present all year round with maximum abundances in the end of summer. The presence of fishes confirms that this kind of wetland plays an important trophic and nursery role for these species. Differences in densities and stages distribution of these species into Mont Saint-Michel systems (tidal mudflats, estuaries and tidal salt marshes) can reduce the trophic competition.

Keywords: fish community; intertidal salt marsh; ecological group; temporal variations; Europe

Introduction

North American salt marshes are known to play a trophic and nursery role for many fishes and macrocrustaceans, including many important fishery species (Shenker & Dean, 1979; Minello & Zimmerman, 1983; Boesch & Turner, 1984; Kneib, 1997*a*). A number of these animals depend, for more or less long periods of their life cycle, on the intense primary productivity and the refuge provided by vascular plants. Comparatively, fish communities using European salt marshes have rarely been studied, although these intertidal habitats play important roles for fish communities (Labourg *et al.*, 1985; Frid, 1988; Frid & James, 1989; Drake & Arias, 1991; Cattrijsse *et al.*, 1994; Laffaille *et al.*, 1998; 1999*a*; 2000). In Europe, mean tide level borders the low marsh (Beeftink, 1977). As a consequence, salt marshes and their creeks are flooded only during high spring tides. Fishes only invaded this environment during short immersion periods of a few minutes to a few hours according to the location on the marsh (Cattrijsse *et al.*, 1994; Laffaille *et al.*, 1998; Lefeuvre *et al.*, 1999). The principal reason of this paucity of research was reportedly the difficulty of sampling and quantifing the density of fish communities in such intertidal habitats (Kneib, 1997*a*, *b*). Thus, in Europe, the nursery locality is usually described as restricted to the mudflats of marine coastal waters such as estuaries and lagoons (e.g. Costa, 1988; Elie *et al.*, 1990; Costa *et al.*, 1994) as is the case in the Mont Saint-Michel Bay (France), where the high salt marsh primary productivity contributes to sustaining an exceptional biodiversity especially in fish and molluscs (Feunteun & Laffaille, 1997). Moreover, the bay's mudflats represent one of the main nurseries of the English Channel coast for many species such as sea bass (*Dicentrarchus labrax*), whiting (*Merlangius*

[a]Corresponding author. Tel: 02 99 28 69 24; fax: 02 99 28 14 58; E-mail: pascal.lafaille@univ-rennes1.fr

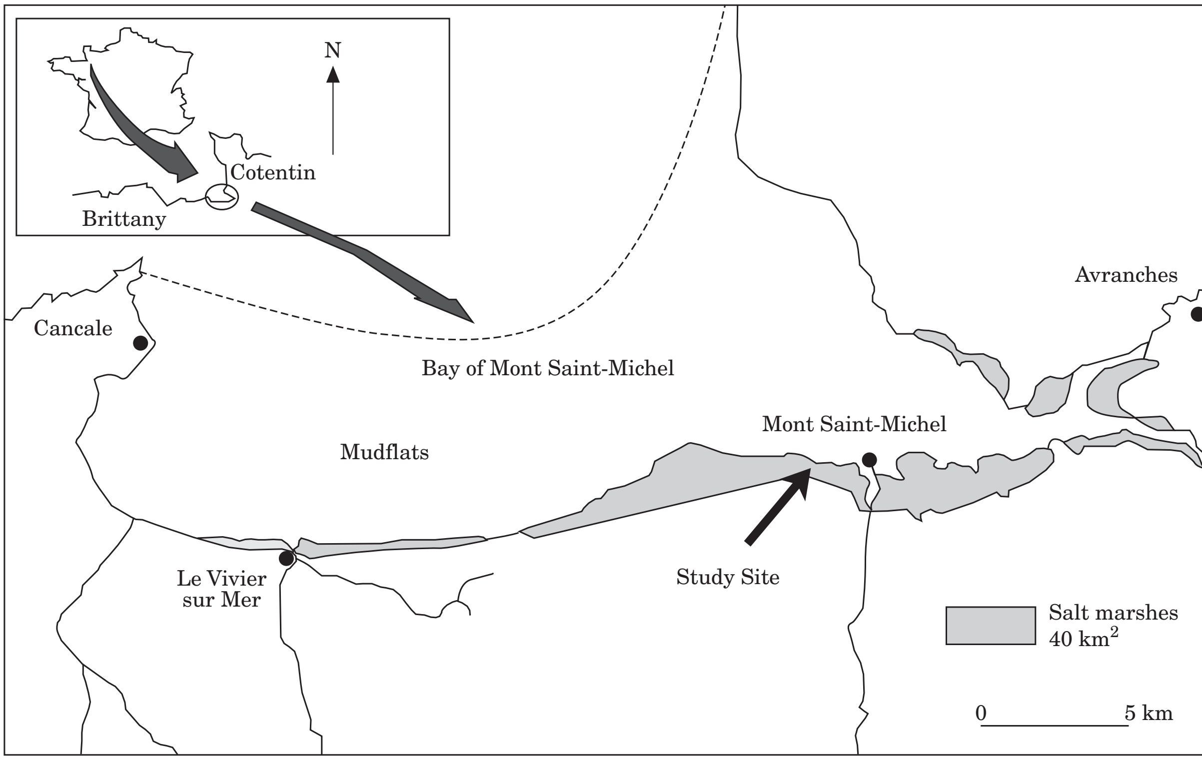

FIGURE 1. Location of the Mont Saint-Michel Bay and study site.

merlangius), flat fishes (*Raja* spp., *Solea solea*, *Pleuronectes platessa*) and clupeids (*Sardina pilchardus*, *Clupea harengus* and *Sprattus sprattus*) (Legendre, 1984; Laffaille *et al*., 1999*b*). Many adult fishes also utilize this environment and sustain a traditional fishery (Beillois *et al*., 1979; Legendre, 1984). The intense productivity of salt marshes (Bouchard, 1996; Bouchard & Lefeuvre, 1996) is also known to be exploited by birds (Schricke, 1983; Lefeuvre *et al*., 1994; 2000) and sheep (Vivier, 1997).

The objectives of this study were: (a) to describe the fish community that colonizes macrotidal salt marshes; and (b) to evaluate these coastal wetland as nurseries and assess their trophic value for fishes compared to other habitats of Mont Saint-Michel Bay and American wetlands. During 3 years, the fish community structure visiting an intertidal creek of these marshes was defined in terms of abundance, ecology and age group. Monthly, seasonal and yearly changes were examined where intertidal salt marshes play trophic and nursery roles.

Material and methods

Study sites

The Mont Saint-Michel Bay (France) is a 500 km^2 littoral zone situated in the Normano-Breton Gulf (latitude 48°40′N, longitude 1°40′W) (Figure 1) with the Abbey of the Mont Saint-Michel situated on top of a promontory in the middle of the bay. The bay is a semi-diurnal macrotidal system with the second highest tidal range in Europe (average: 10–11 m, maximum 16 m). The intertidal zone covers 220 km^2 including 180 km^2 of mudflats and 40 km^2 of salt marshes. Ecological functioning of Mont Saint-Michel Bay has been studied since 1979 (Lefeuvre *et al*., 1994; 2000).

These salt marshes are incised by a dense network of creeks into which sea-water flows during a number of tidal cycles. The study site (Figure 1), located west of Mont Saint-Michel and dominated by *Atriplex portulacoïdes* (Bouchard, 1996; Bouchard & Lefeuvre, 1996), is situated 2·5 km from the coastline on a 10 m wide creek which drains a 5·7 ha watershed. The water only reaches this creek during 43% of the tides when the water level is >11·25 m. Salt marsh vegetation is flooded only when tidal amplitudes are greater than 12·40 m (5–10% of tides). The creek is flooded for 2 h on average (Troccaz *et al*., 1994; Laffaille *et al*., 1998). During the rest of the time, creek and salt marshes remain unflooded. So salt marshes, including tidal creeks and vegetated tidal flats, can be invaded by fishes only during these intermittent high spring tides and for a very short period during each tide. These characteristics are the principal differences from those of north-west American salt marshes which are repeatedly inundated twice a day by tide (Morley, 1973; Beeftink, 1977; McKee & Patrick, 1988).

Sampling the fish community

In salt marshes, fishes were caught in the creek during 120 tides between March 1996 and April 1999, except April 1998, December 1998 and February 1999 due to technical problems. Sampling selectivity was reduced by using (1) fyke net (4 mm mesh size, 5 m deep, 1·80 m high and 20 m wide) to catch small fishes and (2) trammel nets (30–70 mm mesh size, 2 m high and 30 m long) to capture larger fishes, especially mugilids that could jump over the fyke net. Nets were set across the creeks according to the method described by Laffaille *et al.* (1998). Both devices were set in the creek to catch every fish that left the salt marsh during ebb. Sampling was conducted to quantify fish stocks during each tide and to analyse the monthly and seasonal variation of population and community structure. To minimize variations of environmental conditions between each period, two to five samplings were made each month when tidal amplitudes ranged between 11·5 and 12·0 m, during evening ebbs and comparable meteorological conditions (no or little wind and clear sky).

Analysis

All samples were frozen (− 18 °C) until analysis at the laboratory. Fish were identified to species, except for mugilids of less than 100 mm where identification is problematical (Sauriau, 1990). Sources of identification of small mullets (Farrugio, 1977; Reay & Cornell, 1988; Serventi *et al.*, 1996) were conflicting as also suggested by Feunteun (1994). Individual fish was measured to the nearest 1 mm and weighed to the nearest 10 mg to establish the biomass (%B), numeric (%N) and monthly frequency of occurrence (%FO) composition of population and community.

Fish species were separated into the following ecological categories according to Potter *et al.* (1986) and adapted by Feunteun and Laffaille (1997) for Mont Saint-Michel Bay:

(a) *Catadromous*: obligatory migrants from freshwater into the sea to breed;
(b) *Estuarine*: typical species occurring and breeding in intertidal areas and estuaries of the bay;
(c) *Marine estuarine dependent*: marine species which enter the intertidal areas of the bay in large numbers;
(d) *Marine straggler*: marine species abundant in the marine environment but only infrequently found in intertidal areas of this bay.

As proposed by Clark *et al.* (1996), all monthly samples were combined. Temporal fluctuations of the community were analysed by means of cluster analysis on densities (Ward's methods, Euclidean distances). Prior to the statistical analysis the data were log $(x+1)$ transformed (Field *et al.*, 1982).

Results

Composition of fish communities

A total of 250 000 fishes (25 000 analysed), belonging to 31 species and 19 families were caught (Table 1) during the 3 year study. Among these, seven were marine straggler species, 13 were marine estuarine dependant species, three were catadromous species and eight were estuarine species. No anadromous or freshwater species were caught.

All these species do not frequent tidal salt marshes with similarly frequency and abundance. Nine taxa occurred frequently (monthly %FO >50%): four estuarine species (the sand gobies, *Pomatoschistus minutus* and *P. lozanoi*, the three-spined stickleback, *Gasterosteus aculeatus* and the lesser pipefish *Syngnathus rostellatus*); four marine estuarine dependant species (the young mullets, *Mugil* spp., the sea bass, *D. labrax*, and the sprat, *S. sprattus*) and one catadromous species (the thin-lipped grey mullet *Liza ramada*). Marine straggler species occurred at low frequencies (%FO <25%).

Numerical abundance was highly dominated by sand gobies (*P. minutus* and *P. lozanoi* represented respectively 70% and 12%) and secondarily by *D. labrax* (%N = 11%). *Liza ramada* represented 87% of the total biomass. Glass eels and flatfish larvae were under-estimated because the fyke net was not considered as an efficient sampler of these small benthic fishes.

Estuarine species (sand gobies, three-spined stickleback and pipefish) were caught at all stages (alevin, juvenile and adult) (Table 2). Except *L. ramada*, all other marine and catadromous fishes were mainly found at young stages, alevins and juveniles (and especially 0 group).

Monthly variations

The tidal salt marsh was colonized by fish every time the tide reached the creek. The cluster analysis of the monthly samples (combined dates) indicates that the

TABLE 1. Composition of fish community caught in the tidal creek from March 1996 to April 1999. %FO: monthly percentage frequency of occurrence; %B: percentage biomass abundance; %N: percentage numerical abundance

Group	Families	Species	%N	%B	%FO
Marine straggler species					
	Agonidae	*Agonus cataphractus* (L.)	0·00	0·00	2·9
	Belonidae	*Belone belone* (L.)	0·01	0·00	14·3
	Carangidae	*Trachurus trachurus* (L.)	0·00	0·00	2·9
	Gobiesocidae	*Lepadogaster lepadogaster* (L.)	0·00	0·00	5·7
	Gobiidae	*Aphia minuta* (Risso)	0·01	0·00	20·0
		Crystallogobius linearis (Von Düben)	0·01	0·00	5·7
	Scophthalmidae	*Scophthalmus rhombus* (L.)	0·00	0·00	2·9
Marine estuarine dependant species					
	Ammodytidae	*Ammodytes tobianus* (L.)	0·10	0·00	20·0
	Atherinidae	*Atherina presbyter* (Cuvier)	0·04	0·03	20·0
	Clupeidae	*Clupea harengus* (L.)	0·33	0·02	48·6
		Sprattus sprattus (L.)	1·32	0·07	65·7
	Gadidae	*Trisopterus luscus* (L.)	0·00	0·00	2·9
	Liparidae	*Liparis montagui* (Donovan)	0·00	0·00	2·9
	Mugilidae	*Liza aurata* (Risso)	2·00	5·80	74·3
		Mugil sp.	1·57	0·64	91·4
	Pleuronectidae	*Limanda limanda* (L.)	0·10	0·00	8·6
		Pleuronectes platessa (L.)	0·43	0·05	37·1
	Serranidae	*Dicentrarchus labrax* (L.)	11·14	0·99	77·1
	Soleidae	*Solea solea* (Quensel)	0·04	0·00	14·3
	Trachinidae	*Echiichtys vipera* (Cuvier)	0·00	0·00	2·9
Estuarine species					
	Gasterosteidae	*Gasterosteus aculeatus* (L.)	0·33	0·08	74·3
	Gobiidae	*Pomatoschistus lozanoi* (de Buen)	11·50	1·08	94·3
		Pomatoschistus microps (Kroyer)	0·13	0·01	40·0
		Pomatoschistus minutus (Pallas)	69·95	4·20	100·0
	Syngnathidae	*Hippocampus hippocampus* (L.)	0·00	0·00	5·7
		Syngnathus abaster (Risso)	0·00	0·00	8·6
		Syngnathus rostellatus (Nilson)	0·11	0·00	57·1
		Syngnathus typhle (L.)	0·00	0·00	5·7
Catadromous species					
	Anguilidae	*Anguilla anguilla* (L.)	0·13	0·01	42·9
	Mugilidae	*Liza ramada* (Risso)	0·58	87·01	68·6
	Pleuronectidae	*Platichthys flesus* (L.)	0·14	0·02	17·1

community structure showed few differences between the 3 years. In fact, three seasonal groups [Figures 2(a and b)] were identified at the 60% and 75% level on the basis of dissimilarities between species composition and abundance (respectively for number and biomass).

Cluster group A was composed of samples collected from April to June for numbers and from March to June for biomass. It corresponded to spring when fish density was low (average 11 fishes and 6 g per min without *L. ramada*) and species number was maximal (average 10 to 11 species and up to 22 species) (Tables 3 and 4). This season represented the principal recruitment period of marine species (marine stragglers and marine estuarine dependant) in Mont Saint-Michel Bay. In salt marshes, it was especially the case for *P. platessa*, sea bass (March to July), clupeids and young mullets (from 0 to 2 fishes and from 0 to 1 g per species and per min).

Cluster group B was composed of samples collected from July to October and corresponded to summer and autumn. During this period, specific richness (from eight to 19; average 11 species) and densities (average 134 fishes and 871 g per min) were maximal (Tables 3 and 4) with two peaks in September 1996 and in October 1997 (over 280 and 260 fishes per min respectively). It is the period of maximum presence for marine estuarine dependant species, except for flatfish that left the salt marshes in June. The gobies *P. minutus* (average 108 fishes per min) and *P. lozanoi*

TABLE 2. FL: Fork length mean ± standard deviation, min. and max. (FL, mm) of different fish species N: number of measured fish. Species are listed in alphabetical order for each ecological group

Group	Species	FL mean	FL SD	FL min.	FL max.	N
Marine straggler species						
	Agonus cataphractus (L.)	25·0	—	25	25	1
	Aphia minuta (Risso)	35·5	11·9	16	55	37
	Belone belone (L.)	60·7	15·7	37	85	9
	Crystallogobius linearis (Von Düben)	32·1	6·1	19	52	34
	Lepadogaster lepadogaster (L.)	19·0	2·5	14	21	6
	Scophthalmus rhombus (L.)	25·0	2·8	23	27	2
	Trachurus trachurus (L.)	53·0	—	53	53	1
Marine estuarine dependant species						
	Ammodytes tobianus (L.)	34·8	8·0	20	60	107
	Atherina presbyter (Cuvier)	74·6	7·3	45	100	423
	Clupea harengus (L.)	38·0	15·4	20	135	302
	Dicentrarchus labrax (L.)	43·5	25·1	12	275	2822
	Echiichtys vipera (Cuvier)	11·0	—	11	11	1
	Limanda limanda (L.)	12·3	1·2	9	15	150
	Liparis montagui (Donovan)	21·0	1·4	20	22	2
	Liza aurata (Risso)	136·9	20·6	100	395	560
	Mugil sp.	34·1	9·8	14	100	5034
	Pleuronectes platessa (L.)	35·5	12·7	9	232	135
	Solea solea (Quensel)	12·8	3·0	8	56	46
	Sprattus sprattus (L.)	35·7	7·0	19	86	1951
	Trisopterus luscus (L.)	61·1	25·3	13	76	10
Estuarine species						
	Gasterosteus aculeatus (L.)	44·4	16·0	15	68	907
	Hippocampus hippocampus (L.)	75·5	68·6	23	120	2
	Pomatoschistus lozanoi (de Buen)	31·1	7·3	9	74	3372
	Pomatoschistus microps (Kroyer)	45·9	8·5	18	70	75
	Pomatoschistus minutus (Pallas)	35·7	10·1	7	75	6453
	Syngnathus abaster (Risso)	71·6	16·6	36	82	7
	Syngnathus rostellatus (Nilson)	81·4	18·3	34	140	302
	Syngnathus typhle (L.)	95·8	7·6	83	103	5
Catadromous species						
	Anguilla anguilla (L.)	69·7	4·9	54	145	196
	Liza ramada (Risso)	393·1	61·9	136	525	1452
	Platichthys flesus (L.)	46·2	45·6	10	210	35

(average 14 fishes per min) were abundant and colonized salt marshes after reproduction. *Liza ramada* was abundant (1 fish and 773 g per min); it is the preferential period of presence (from July to October) in brackish systems.

Cluster group C was composed of winter samples collected from November to February for biomass and from November to March for number. During this period, specific richness (from six to 14 species; average seven species) and biomass (average 50 g per min) were low (Tables 3 and 4). Only sand gobies (average 42 fishes per min), *G. aculeatus* (0·8 g per min) and young mullets (4 g per min) were common. *Anguilla anguilla* were always present at this time of their anadromous migration.

Discussion and conclusion

Fish community

At least 100 fish species have been recorded in the tidal mudflats of Mont Saint-Michel Bay and estuaries (Lam Hoi, 1967; Beillois *et al.*, 1979; Legendre, 1984; Feunteun & Laffaille, 1997; Laffaille *et al.*, 1999*b*). Among the 31 species that colonized particularly the tidal salt marshes, three were catadromous, seven were marine stragglers, 13 were marine estuarine dependant and eight were estuarine. Not one typical freshwater species was caught in marsh creeks, despite the frequent occurrence of bream (*Abramis brama*) and bleak (*Alburnus alburnus*) in tidal estuaries close to

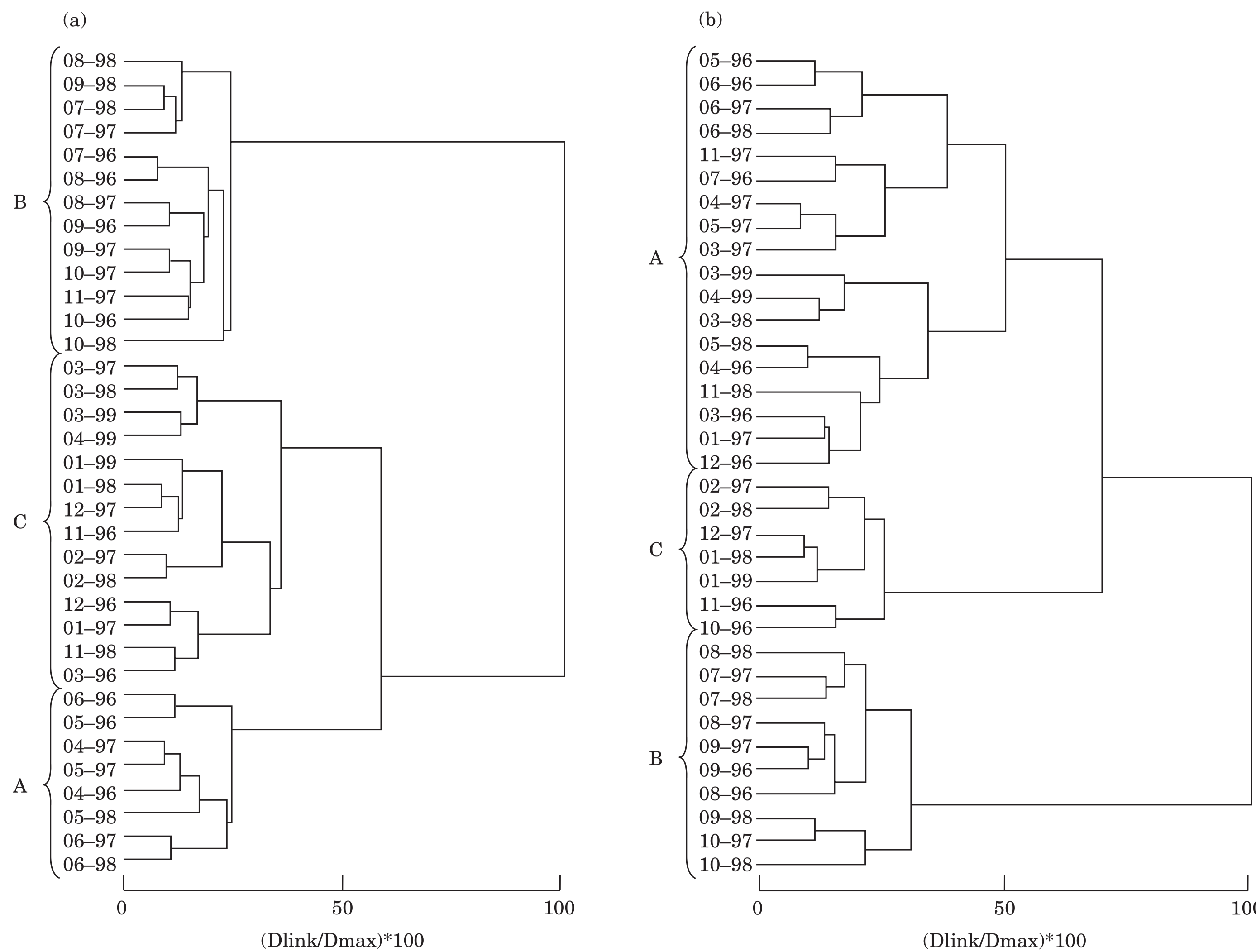

FIGURE 2. Cluster analysis (Ward's Method, Euclidean distances) on the log (x+1) transformed monthly densities (a) and weights (b) (combined all monthly samples) of species recorded between March 1996 (03–96) and April 1999 (04–99). The linkage distance (Dlink) is presented as a percentage of the maximum linkage distance (Dmax).

TABLE 3. Seasonal variations of composition and numerical abundance (mean CPUE ± standard deviation) of fish community sampled between March 1996 and April 1999. Seasons were identified with cluster analysis (see material and method and Figure 2). CPUE: number of fish caught per min

Species	Spring		Summer–autumn		Winter	
	mean	SD	mean	SD	mean	SD
A. anguilla	0·0	0·1	0·0	0·0	0·2	0·4
C. harengus	0·4	1·2	0·4	0·5	0·0	0·8
D. labrax	0·3	0·7	3·5	2·6	0·2	0·6
G. aculeatus	0·2	0·2	0·1	0·3	0·3	0·4
L. aurata	0·3	0·6	3·7	4·4	0·4	0·7
L. ramada	0·2	0·2	1·1	1·5	0·0	0·2
Mugil sp.	2·0	2·0	0·6	1·6	1·1	1·7
P. lozanoï	1·1	1·3	14·7	19·8	7·9	8·7
P. microps	0·0	0·0	0·1	0·2	0·2	0·3
P. minutus	3·0	3·1	108·0	71·1	34·9	54·7
P. platessa	1·2	1·6	0·0	0·0	0·0	1·2
S. rostellatus	0·2	0·1	0·1	0·0	0·0	0·2
S. sprattus	1·2	2·0	1·9	1·7	0·0	1·3
Total CPUE	11·0	4·3	134·2	77·9	45·5	62·1
Number of species	11·1	5·3	10·8	3·3	7·5	4·5

TABLE 4. Seasonal variations of composition and biomass abundance (mean CPUE ± standard deviation) of fish community sampled between March 1996 and April 1999. Seasons were identified with cluster analysis (see material and method and Figure 2). CPUE: g of fish caught per min

Species	Spring		Summer–autumn		Winter	
	mean	SD	mean	SD	mean	SD
A. anguilla	0·0	0·0	0·0	0·0	0·1	0·1
C. harengus	0·1	0·3	0·1	0·2	0·0	0·1
D. labrax	0·7	1·8	8·6	6·9	1·6	3·0
G. aculeatus	0·0	0·0	0·1	0·5	0·8	0·7
L. aurata	0·8	1·2	57·4	66·4	5·4	12·1
L. ramada	153·7	218·7	773·0	1183·1	2·8	7·8
Mugil sp.	0·9	1·6	2·7	9·2	3·8	11·3
P. lozanoï	1·2	1·5	4·0	4·6	7·6	8·3
P. microps	0·0	0·1	0·0	0·1	0·1	0·1
P. minutus	1·4	2·0	23·8	20·0	24·1	39·0
P. platessa	0·4	0·9	0·0	0·0	0·1	0·3
S. rostellatus	0·0	0·0	0·0	0·0	0·0	0·0
S. sprattus	0·2	0·3	0·5	0·6	0·0	0·0
Total CPUE	159·7	219·9	870·5	1244·6	46·7	50·3
Number of species	10·3	4·9	10·8	3·3	7·4	3·4

salt marshes (Legendre, 1984; Laffaille *et al*., 1999*b*), which are limited by marine currents and high salinity (between 10 and 35 salinity). Sand gobies (especially *P. minutus*) were numerically dominant (more than 80% of fishes sampled) and mullets (especially *L. ramada*) were dominant in term of biomass (more than 90% of biomass sampled). Other studies confirm the dominance of a small number of species in creek marsh communities (Kneib, 1987; Sogard & Able, 1991; Cattrijsse *et al*., 1994; Kneib, 1997*a*, *b*). *Pomatoschistus* spp. are among the most abundant species of western European tidal areas and represent important prey for predators of the coastal food webs (see Hamerlynck *et al*., 1993; Hamerlynck & Cattrijsse, 1994). In Mont Saint-Michel Bay, these species are among the most dominant in mudflats, salt marshes and estuaries (Laffaille *et al.*, 1998; 1999*a*, *b*; this study). Most often in north-east American salt marshes, the dominant species are estuarine, particulary *Fundulus heteroclitus* (Allen, 1982; Peterson & Turner, 1994; Kneib, 1995, 1997*a*). *Pomatoschistus* spp. in Europe occupy a comparable niche to that of *F. heteroclitus* in north American salt marshes (Kneib, 1986).

Length frequency analysis indicated that 0-group dominated the fish community of marsh creeks whereas in tidal mudflats and in estuaries 1 and 2-group dominated (Legendre, 1984; Laffaille *et al.*, 1999*b*). Labourg *et al.* (1985) has observed a similar spatial separation between tidal salt marshes and mudflats in Arcachon Bay (France), especially for mullets, sea bass and common soles (*Solea solea*).

In Europe, mean tide level borders the low marsh (Beeftink, 1977). As a consequence, salt marshes and their creeks were flooded only during high spring tides. Fishes only invaded this environment during short immersion periods of a few minutes to a few hours according to the location on the marsh (Cattrijsse *et al.*, 1994; Laffaille *et al.*, 1998; Lefeuvre *et al.*, 1999). So, no species can be considered as marsh resident.

Some samples were taken from other creeks of these tidal salt marshes. Composition of fish assemblages were very similar, varying slightly (Laffaille *et al.*, 1999*b*), only because of different local conditions. Therefore, it can be concluded that tidal creeks of salt marshes of Mont Saint-Michel Bay, as elsewhere in many European localities, are dominated by the estuarine fishes *Pomatoschistus* spp. and marine estuarine dependant species such as mullets, young sea bass and young flatfishes (*P. platessa*, *S. solea* and *Platichthys flesus*) (Labourg *et al.*, 1985; Frid, 1988; Frid & James, 1989; Drake & Arias, 1991; Cattrijsse *et al.*, 1994; Laffaille *et al.*, 1998; this study), local variations however are mostly attributable to differences of many factors including collecting gear and geographic location (Kneib, 1997*a*). In each case, specific richness decreased from mudflats to salt marshes (in Mont Saint-Michel bay, 100 species in mudflats *vs* 31 species in salt marshes). In fact, this environment is characterized by important short-term fluctuations of abiotic factors such as water temperature, salinity, oxygen concentration, tidal current speed and direction to which no fish are specifically adapted. Most species exploiting the high primary and secondary productivity of this wetland are euryhaline and eurythermal migrants such as mullets, gobies, young sea bass and flatfishes (Laffaille *et al.*, 1998, 1999*a*; 2000).

Temporal variations

The structure of the fish community that colonizes tidal creeks of the bay is relatively stable on a yearly basis. As in many European and north American salt marshes, colonization varies according to seasons (Cain & Dean, 1976; Weinstein, 1979; Cattrijsse *et al.*, 1994) and to life-history stage (Bozeman & Dean, 1980; Talbot & Able, 1984; Kneib, 1987). In Mont Saint-Michel Bay, the structure showed three seasonal phases, namely spring, summer clustered with autumn, and winter. Seasonal trends also vary according to ecological groups.

Estuarine species occurred all year long, as they follow tidal currents in order to exploit the tidal flats including mudflats, salt marshes and estuaries (Feunteun & Laffaille, 1997; Laffaille *et al.*, 1999*a*, *b*). Size structures and densities varied essentially according to reproduction periods (end of spring to beginning of summer) and monthly mortality rates (Laffaille *et al.*, 1998). Such species are probably migrants between salt marshes, mudflats and estuaries, according to local conditions, stages and reproductive cycles (Fonds, 1973; Hestagen, 1977; Kedney *et al.*, 1987; Bouchereau *et al.*, 1989; Whoriskey & Fitzgerald, 1989).

Marine estuarine dependent species did not occur from mid-autumn to the beginning of spring. Densities were maximal from the end of spring to the beginning of autumn at temperatures of 14–21 °C. During the cold season, most marine estuarine dependent fishes probably migrate to offshore areas where water temperature is higher (Claridge & Potter, 1983; Aprahamian & Barr, 1985; Rosecchi & Crivelli, 1995). Catadromous species colonize creeks during their preferred period of migration inshore.

In the Mont Saint-Michel Bay, tidal mudflats, tidal salt marshes and estuaries play a significant nursery role for fish communities. Dominant species are young marine estuarine dependent fishes and estuarine fishes of all stages. Evidently in the bay, the fish exploit all food that sustains an important part (for marine estuarine dependant fishes) or the total part (for estuarine fishes) of their growth. Spatial and temporal variation in exploitation of these habitats may reduce trophic competition between species and between stages that have similar diets and consequently favour their growth. Understanding the function of each habitat (estuaries, tidal mudflats and tidal salt marshes) and the relation between them in a heterogeneous environment, and especially their effects on abundance, movements and growth of the associated fish fauna is essential for management of entire ecosystems such as that of the Mont Saint-Michel Bay.

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